As regards the systematic position and significance of the species here introduced, it would seem, in the modification of its denticles, to indicate a slightly closer relationship to the ordinary forms of the Annelida than the other representatives of the genus, stylate setæ set in elevated prominences being of such general occurrence throughout the *Errantia* and *Tubicola*.

XXIX.—*On the Pairing of Zoospores, the Morphologically Fundamental form of Reproduction in the Vegetable Kingdom.*

By N. Pringsheim*.

The author states that he has previously shown, from observations on some genera of the *Zoosporeæ*, that those reproductive cells which had been considered resting-spores are the female reproductive organs. The male organs in some genera have the form of small bodies more or less differing from the zoospores; in other genera they are so like the zoospores that they appear to be only smaller forms of the latter.

The views thence derived with regard to the multiplication and reproduction of these plants might be assumed to be applicable to all those *Zoosporeæ* in which two forms of zoospores are known, and in which the existence of resting-spores is known or suspected.

But in most genera of Algæ in which zoospores exist, resting-spores have not yet been discovered; and in those genera in which two forms of zoospores are known, it has been assumed that both kinds are of the same nature, and that they germinate without any sexual act. The author has shown that in some genera which have two kinds of zoospores and no resting-spores, the small zoospores, passing into a state of immobility, become themselves resting-spores, and that these resting-spores, produced by the so-called microgonidia, reproduce the mother plant.

These different views must admit of being reconciled, unless it be assumed that essential differences in the mode of increase and reproduction exist in such nearly allied plants. If it be not assumed that all the plants without resting-spores are asexual, it must follow either that their resting-spores remain to be discovered (which is improbable), or that in the *Zoosporeæ*, and in their already known organs, the sexual act takes place in a special manner not yet discriminated. The

* From the 'Monatsbericht' of the Royal Academy of Sciences of Berlin, Oct. 1869.

existence of two kinds of zoospores in the same plant seemed to afford a clue to the discovery of this unknown sexual act.

The discovery announced in this paper is that of a modification of the sexual act, forming a link between the known forms of reproduction, and showing that the different sexual products are a series of variations, passing into one another, of one and the same form. This modification is here called "pairing of zoospores;" and the essential difference between this and other processes of reproduction lies in the appearance of motile brood-spheres*, which are externally just like the zoospores.

The plant in which this modification occurs is *Pandorina Morum*, a plant the different states of which have given rise to a number of groundless and confusing genera, and which is often confounded with another nearly allied Volvocine, *Eudorina elegans*.

Until the appearance of the phenomena introductory to reproduction, the plants are distinguishable by the form and arrangement of their green cells. *Pandorina* has somewhat wedge-shaped cells. The base of the wedge is turned outwards; and the cells, which are in close connexion with one another, entirely fill the oval cavity which is enclosed by the general envelope of the plant. *Eudorina*, on the other hand, has spherical cells arranged in a single layer at the periphery of the envelope, and at regular, almost equal, distances from one another. The structure of the cell is identical in both plants, and similar to that in the other *Volvocineæ*.

The number of cells in *Pandorina* is typically sixteen, occasionally less, in *Eudorina* thirty-two, sometimes fewer.

Asexual reproduction takes place in *Pandorina*, as in other multicellular *Volvocineæ*, by the formation of a perfect young plant in each cell of the mother plant. By the gradual dissolution of the general envelope and of the special membrane of the mother cells, the young plants become free and escape.

In sexual reproduction, as in the asexual, the membrane of the old plant swells, and sixteen young plants are formed. The young plants, however, are (at least in part) not neuter, but sexual, and either male or female. Whether the mother plant is monœcious or diœcious is difficult to determine, because the male and female plants are externally alike, and can hardly be distinguished with certainty during copulation. There is no striking difference in structure between the sexual and asexual plants, although, amongst the former, plants with

* [It is difficult to translate the German word "Befruchtungskugel." It is used to express the spore or globular mass of protoplasm before it has been fertilized by the action of the spermatozoids.—Tr.]

less than sixteen cells, especially with eight cells, are oftener produced. Moreover the dissolution of the membrane of the mother cell proceeds more slowly than in the case of neuter plants, one result of which is that the young sexual plants vary much in the extent of their growth, and continue united in groups of different sizes for a long time after their formation, according as a greater or less number of them have happened to become free from the gelatinous mass in which they were imbedded.

As the individual groups are at first motionless, and the mother plant loses its cilia during the formation of the young ones, the entire group is at first entirely quiescent. But afterwards the young sexual plants, like the neuter ones, produce upon each of their cells two cilia, which commence their motion as soon as the enveloping mucus admits of it; and thus ultimately the entire group assumes a state of active rotation. During the rotation of the groups the same process of expansion and dissolution takes place in the membrane of the sexual plants as occurred in the mother plant; but the contents of the cells of the sexual plants do not undergo division, but combine to form a single zoospore, which becomes free by the rapid dissolution of the membranes.

In their general structure these zoospores differ in no way from other zoospores. At their colourless apex they exhibit, like other zoospores, a red body placed on one side of the apex, and two long vibrating cilia, by which they move in the manner common to zoospores.

The individual zoospores exhibit no marked differences, except that (like the sexual plants from which they spring) they vary in size within tolerably wide limits, but not in a manner to indicate the existence of two different sorts.

Amongst the groups of isolated zoospores of different sizes, some are at last seen to approach one another in pairs. They come into contact at their anterior hyaline apex, coalesce with one another, and assume a shape resembling a figure of 8*. The constriction which marks their original separation disappears by degrees; and the paired zoospores form at last a single large green globe, showing at the circumference no trace of their original separation. It may be seen, however, that the globe is larger than the individual neighbouring zoospores, that it has a strikingly enlarged colourless mouth-spot, with two red bodies on the right and left, and that it is furnished with four vibrating cilia originating in pairs near the

* [The German expression is "biscuit-artige Gestalt," but this, if translated literally, would convey no idea to an English reader.—Tr.]

two red spots. The four cilia, however, soon become motionless, and, together with the red spots, disappear.

This act of conjugation occupies some minutes, *i. e.* from the first contact of the zoospores to the formation of the green globe. The latter becomes the oospore, which, after growing slightly larger and assuming a red colour, germinates after a long period of rest, and brings forth a new *Pandorina*.

There is hardly any appreciable difference, except in size, and that to no reliable extent, between the male and female zoospores. Most frequently a small zoospore pairs with a larger one; but two of equal size (either of the larger or smaller forms) often unite. Probably both the females and the males vary much in size, the former more so than the latter.

With regard to the entire plants from which the zoospores are produced, there is little doubt that those of the largest size are females; but the sex of the smaller and middle-sized ones cannot be determined with any certainty.

The germination of the oospore is like that of other *Volvocineæ*, especially resembling in its early stage the germination of the resting-spores produced by the microgonidia of *Hydrodictyon utriculatum*. The oospore bursts and produces a single large zoospore (in rare cases two, or even three), which divides into sixteen cells and becomes a young *Pandorina*.

[The author then remarks that Cohn (in *Volvox*) and Carter (in *Volvox* and *Eudorina*) describe the spermatozoids as differing materially from the zoospores, and that they speak of the brood-spheres as globular resting-cells. Whilst suggesting some possible modes of reconciling the observations of Cohn and Carter with his own on *Pandorina*, the author admits that further investigation of *Volvox* and *Eudorina* is necessary.]

A comparison of the relations between the sexual act in *Pandorina Morum* and that in other plants seems to afford a clear insight into the gradual changes in the sexual products and the sexual act in plants.

Hitherto the conjugation of the *Zygosporeæ* has appeared to have no affinity with the sexual act in other Algæ; and these plants seemed, therefore, to form a sharply defined separate group.

Considering that in most plants the sexual organs differ much in form and size, the doubts as to the copulation of the *Zoosporeæ* seemed reasonable. The pairing of the zoospores which takes place in *Pandorina* with hardly even an incipient differentiation of the sexual organs, seems to be a fresh instance of the act of copulation occurring in plants with motile sexual organs, and it forms, therefore, a bridge between the *Zygosporeæ* and the *Zoosporeæ*; and perhaps a more complete

knowledge of the mode of conversion of the microgonidia into resting-spores in the *Chætophoreæ*, and especially in *Draparnaldia*, will disclose the peculiar bond of union between these two divisions of the Algæ.

Whilst this pairing is connected, on the one hand, with the copulation in the *Zygosporeæ*, it is still more closely allied, on the other hand, with the known sexual process in the *Zoosporeæ*.

Comparing the sexual act in *Pandorina* and *Œdogonium*, we find that the anterior, colourless, protoplasmic mass of the brood-sphere of *Œdogonium*, in front of which, as in *Pandorina*, the coalescence with the spermatozoid takes place, is identical with the so-called "mouth" (*Mund-Stelle*) of one of the two pairing zoospores of *Pandorina*, and with the so-called "mouth" of the directly germinating zoospores of *Œdogonium*. It may be taken to be undeniable that the resting brood-spheres of *Œdogonium*, as well as those of *Vaucheria* and *Coleochæte*, to which those of other Algæ which have a less defined or hardly perceptible germ-spot are closely allied, are only unciliated resting-forms of zoospores.

But the analogy of the structure of the brood-sphere and the zoospore may be extended far beyond the Algæ.

It would seem to be a result of the foregoing that that which in the embryonic vesicle of the Phænogams has been called by Schacht the filamentary process (*Faden-Apparat* *) is an analogue of the colourless "locus of impregnation" (*Befruchtungstelle*) in the brood-spheres of Algæ, and of the mouth or germ-spot of the zoospores. The canal-cell observed in the central cell of the archegonium of *Salvinia*, and which seems to occur also universally in mosses and ferns, is a corresponding organ. The word "germ-spot" (*Keimfleck*) would be a convenient word to express the locus of impregnation of female plants in general, which term would include the "mouth" of the zoospores, the colourless protoplasmic

* ["*Faden-Apparat*" is the term used by Schacht to describe the anterior portion of the germinal vesicle in *Crocus Watsonia* and some other plants. He imagines that it exists in all plants in which the pollen-tube does not penetrate the embryo-sac, and he describes it as consisting of delicate cellulose threads radiating downwards. Schacht's observations have been questioned by Hofmeister, but were partly confirmed by the late Professor Henfrey. The reader may refer to Schacht's papers on the impregnation of *Gladiolus segetum* (Bot. Zeitung, Jan. 15, 1858), on the impregnation of *Crocus vernus* (Regensb. Flora, Sept. 21, 1858), and on the impregnation of *Santalum album* (Pringsheim's 'Jahrbücher für wiss. Bot. vol. iv. p. 1), also to Hofmeister's remarks in the 'Bonplandia' for 1856, p. 287, and in Pringsheim's 'Jahrbücher für wiss. Bot.' vol. i. p. 162, and to Professor Henfrey's paper on "the Development of the Ovule of *Santalum album*," in Trans. Linn. Soc. vol. xxii.—Tr.]

mass at the fore end of the brood-spheres, the canal-cell of the higher Cryptogams, and the filamentary process (*Faden-Apparat*) in the embryonic vesicle of Phænogams.

Those cases amongst the Algæ where, as in *Œdogonium* and *Pandorina*, the entire mass of the brood-sphere, including the whole of the germ-spot, is employed in the formation of the embryo, are introductory to the procreative act in *Vaucheria*, where a portion of the germ-spot is pushed away and cast off before impregnation; and through *Vaucheria* and the analogous formative process in *Coleochæte* the passage is direct to the canal-cell and the filamentary process. Thus the zoospore appears as the ground-form of the embryonal rudiments in the vegetable kingdom; and in the formation of these there is a striking analogy to the phenomena which, in the formation of the embryo in animals, are distinguished as total and partial segmentation.

It may also be worth while to call attention to the fact that, in comparing embryonic vesicles and zoospores, the position of the brood-sphere before impregnation throws light upon the direction of the root of the embryo in those plants in which an embryo is the result of the procreative act, inasmuch as the germ-spot, which from *Œdogonium* up to the Phænogams is without exception turned towards the sexual aperture, corresponds, as the zoospores show, to the *foot* of the germ.

But it being the fact (as is shown by the spermatozoids of *Œdogonium* and *Pandorina*) that the differences in form which have been hitherto attempted to be established between spermatozoids and zoospores have only a relative value as modifications of the same primary form, it will follow that the form of the zoospore, in which even the oldest observers noticed a connecting link between the vegetable and animal kingdoms, may be recognized as the ground-form of all reproductive bodies in plants, and thus an embryological unity may be distinguished in the vegetable kingdom, unless the mode of copulation of the *Florideæ* and the *Fungi* should turn out to be very divergent, as to which further observations must decide.

It is probable that a number of ill-understood phenomena and of unintelligible contradictions of reliable botanists as to the form and colour of microgonidia, as to the number of their cilia, as to their behaviour after the cessation of their mobility, and, lastly, probably, as to double spores, may be fully explained by the supposition of the process of pairing.

It should now be the object of those observers who are occupied in investigating the development of Algæ to look for the phenomenon of "pairing," or for motile brood-spheres, in

all those *Zoosporeæ* in which hitherto zoospores only have been found.

The following is a short summary of the results of this paper:—

1. In the division of the *Zoosporeæ* there are to be found motile brood-spheres which appear in the form of zoospores.

2. The resting brood-spheres are more or less abnormal forms of the zoospore, devoid of cilia.

3. The colourless anterior end of the brood-spheres of Algæ, the "canal-cell" of the higher Cryptogams, and the "filamentary process" of Phænogams are structures which are morphologically identical with the so-called mouth, germ-spot, or, what is the same thing, the *foot* of the zoospore.

4. By analogy to the phenomena of total and partial segmentation in animal ova, it happens in plants that sometimes the entire mass of the brood-sphere is appropriated to the formation of the embryo, sometimes only a portion of it; in the latter case there occurs an entire (?) or partial casting-off of the colourless foot of the brood-sphere, which casting-off occurs sometimes before (as in *Vaucheria*, *Coleochæte*, and *Salvinia*), sometimes after (?) impregnation (as in Phænogams).

5. The remarkable phenomenon that the zoospore is the morphologically fundamental state of the reproductive organs, is an argument for the embryological unity of the vegetable kingdom, and shows that there is a morphological as well as a histological point of contact between it and the animal kingdom.

XXX.—*A last word in Reply to* Dr. Chapman *and* Mr. Frederick Smith *on the Relations of the Wasp and* Rhipiphorus. By Andrew Murray.

The subject has now been so fully ventilated that further discussion seems unnecessary. We have reached that stage when little more can be said on either side until further observation shall have given us fresh materials to argue from. The discussion which has taken place, however, has been of good service in clearing away irrelevant matter, and showing us where the pinch really lies. I trust that Dr. Chapman may have every success in his researches during the ensuing summer; and should he succeed in proving me to be in the wrong, I promise to make him my fullest and handsomest acknowledgments.

To Mr. Smith I have still an answer to make.